# Limited independent flexion of the thumb and fingers in human subjects

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1. We investigated whether human subjects can activate selectively flexor pollicis longus (FPL) and digital portions of flexor digitorum profundus (FDP). These muscles were selected because they are the only flexors of the distal phalanges.

2. Electromyographic activity (EMG) was recorded with intramuscular electrodes from one digital component of the deep flexors ('test') while subjects lifted weights by flexing the distal interphalangeal joint of the other digits in turn ('lifting' digits). Only recording sites at which single motor units were recruited selectively at low forces were used. The weights lifted represented 2·5–50% of the maximal voluntary contraction (MVC). We measured the lowest weight lifted which produced phasic and tonic coactivation in the 'test' muscle.

3. The extent of coactivation varied with the 'distance' between the test and lifting digits although no significant difference occurred in the pattern of coactivation thresholds among the digital flexors. The extent of coactivation increased when angular displacement or velocity at the distal interphalangeal joint of the lifting digit increased but was not critically dependent on restraint of the hand.

4. Because mechanical 'connections' could interfere with the ability to move a distal phalanx independently, the arms of nine cadavers were studied. The separation of tendons between the thumb (FPL) and the index portion of FDP, and between the index and middle portions of FDP, usually extended more proximally in the forearm than separation between the tendons to the middle and ring fingers and between the ring and little fingers. Direct intertendinous links were also noted.

5. It is not possible to direct a sufficiently focal motor command to flex selectively the distal joint of the fingers and thumb when forces exceeding 2·5% MVC are generated. For the middle, ring and little fingers in particular, movement of adjacent digits may also involve 'in-series' mechanical links between adjacent components of FDP.

The ability to flex a single joint of one digit in the hand without movement of adjacent digits requires the ability to contract selectively muscles (or portions of muscles) acting on individual digits. Any limitation in the ability to 'fractionate' movements would derive from neural factors related to motoneurone recruitment and from mechanical linkages between anatomically distinct muscles and digital portions of muscles with multiple tendons. The ability to move a whole digit in isolation is not present in monkeys (Schieber, 1991): with the hand in a neutral position and the interphalangeal joints in some flexion, monkeys were unable to flex one digit without moving the others, despite months of training. This lack of independence was observed for all digits, although to a lesser extent when the thumb and index moved. Schieber (1991) concluded that the lack of independence may reflect properties of the corticomotoneuronal projections which diverge to synapse on motoneurone pools of several muscles (Shinoda, Yokota & Fukami, 1981; see also Fetz & Cheney, 1980; Buys, Lemon, Mantel & Muir, 1986). If the lack of independence in digit movement was related to limited neural control of the relevant muscles, then electromyographic activity (EMG) would appear in the flexor motor units of both the finger instructed to move and adjacent digits.

Although humans have a greater ability to move their digits independently than non-human primates (Napier, 1980), the exact magnitude of this ability in humans is not known. A lack of fractionated movement may reflect an inability to activate selectively particular muscles on the hand. Using transcranial stimulation and recording from the lowest threshold motor units, Gandevia & Rothwell

(1987) showed that, given biofeedback, human subjects were able to deliver 'subthreshold' motor commands selectively to single intrinsic hand muscles. By contrast, this ability could not be learned for pairs of forearm muscles. Thus, even though differentiation of the extrinsic muscles and tendons that act on the hand is greater in human than non-human primates (Marzke, 1992; Serlin & Schieber, 1993), the long flexors acting on the distal interphalangeal joints of the fingers may not be controlled in a fully independent way.

The present study was designed to investigate the extent of independence between the muscles which flex the distal interphalangeal joints of the digits, i.e. flexor pollicis longus (FPL) and the four digital portions of flexor digitorum profundus (FDP). The hand was carefully stabilized to minimize co-contraction and to eliminate the action of the extensor mechanism. Subjects flexed the distal joint of each digit in turn against known loads while low-threshold motor unit activity was monitored. Because digits adjacent to the one required to flex occassionally moved, we assessed the mechanical linkages between adjacent digits during voluntary contractions and during complete paralysis. A preliminary account has been presented (Kilbreath & Gandevia, 1993*a*).

## METHODS

Detailed electromyographic activity (EMG) was recorded in seven subjects studied on three to five occasions. To assess the independence between FPL and FDP, intramuscular EMG was recorded from one deep flexor muscle, i.e. the 'test' muscle (acting on the 'test' digit), while the subject used the other four digits to lift weights. The digit that lifted the weights is referred to as the 'lifting' digit. This nomenclature assumes that each digital portion of FDP constitutes a 'muscle', an issue considered in Discussion. Informed consent was given prior to the experiments and the procedures were approved by the local ethics committee.

### Experimental design

Prior to the EMG studies, the subject's maximal voluntary force for each muscle was measured in brief isometric contractions (MVC). The right hand was positioned so that a subject could only exert force through flexion of the distal phalanx of a particular digit. Three MVCs were recorded for each digit and the peak for each digit was used in calculations. Usually the three values did not differ by more than 10% and, if they did, a subject was retested.

After the recording electrodes were inserted (see below), the subject's hand was positioned so that FPL and FDP were not required to stabilize the hand at rest or when a weight was lifted. The hand posture has been described previously (see Fig. 1 of Kilbreath & Gandevia, 1993*b*). In brief, the hand rests on a table with the fingers loosely positioned around a vertical pillar. The interphalangeal joint of the thumb rests on a horizontal bar on top of the pillar and weights can be lifted by flexion of the tip against a see-saw. For flexion of the finger tips, a band is placed around the distal phalanx and a restraining bar clamps all middle phalanges to the pillar. The extensor mechanism of all fingers is disengaged by this posture (e.g. Gandevia & McCloskey, 1976). Anaesthesia of the radial nerve was not used in this study to paralyse the extensors of the thumb, as this procedure has previously been shown to have only minimal effects on perception of heaviness of weights lifted by FPL (Gandevia, McCloskey & Potter, 1980). Furthermore, the study deliberately aimed to examine the independence of finger control when the usual feedback was present.

Subjects were instructed to lift a weight by flexion of one digit at the distal interphalangeal joint while the other digits were 'relaxed'. A potentiometer attached to the lifting apparatus provided feedback on an oscilloscope so that subjects could keep their lifts consistent. This signal indicated the speed, amplitude and duration of each lift and the different phases of the movement, i.e. lift, hold, and replace. The weights represented 2·5, 5, 10, 15, 20, 25, 35 and 50% MVC for that muscle. Subjects did not necessarily lift all eight weights with each digit: weights were increased or decreased until the minimal weight which produced consistent coactivation in the test muscle was identified (see below). The procedure was then repeated with another digit until all but the test digit had lifted weights. The process was repeated for each muscle and usually one or two test muscles were investigated in an experimental session. The subject lifted the weights through a range of approximately 20–25 deg at the distal interphalangeal joint for the first to the fourth digits, and the fifth digit lifted through a slightly smaller range (i.e. 18–22 deg). The mean angular velocities at which weights were lifted were in the range of 100–250 deg $s^{-1}$.

To compare the relative force levels which produced coactivation when different digits lifted weights, subjects were instructed to lift the weights at the same angular velocity and through the same angle. The effect of the velocity and amplitude of movement was investigated for forces at or just below those in which there was consistent coactivation in the test muscle. Subjects lifted the weights repeatedly through the same angular range at two self-selected velocities. Alternatively, they lifted a weight at the same angular velocity but through different angles (equivalent to 1/4, 1/2, 3/4 and all of the active range of joint flexion).

Additional tests were undertaken to assess whether stability of the hand and fingers affected the force which produced coactivation. The restraint which held the middle phalanges against the vertical rod around which the fingers were comfortably curled was occasionally removed. Also, the effect of stabilizing the forearm and the proximal phalanx of the thumb was assessed.

### Data acquisition and electrode sites

Intramuscular electrodes were made from two strands of Teflon-coated stainless-steel wire (75 $\mu$m diameter), threaded through a short-bevel spinal-tap needle (50 mm length, 25 gauge) with up to 2 mm of insulation removed. EMG was amplified (Medelec PA63 and AA6 MKIII), filtered (bandwidth 80 Hz–3·2 kHz), and 'integrated' (200 ms time constant, Neotrace integrator, model No. NT124A). The EMG and potentiometer signals were displayed on an oscilloscope from which on-line records could be made (Gould ES2000) and stored on tape for reanalysis (Vetter digital PCM 4000A). The filtered EMG was also connected to a dual window and time discriminator with delay (BAK DDIS-1), so that the shapes of at least the first two recruited motor units of the test muscle were identified and displayed on other oscilloscopes (0·5 ms per division). The shapes of these units were used to check

that the electrodes had not moved and they usually remained stable for up to 2 h. To identify them, subjects were provided with audio feedback which was then withdrawn for the main study.

The electrodes for digital portions of FDP were inserted at the mid-forearm level with those for FPL inserted 10–15 mm more distally. The insertion sites for FPL and index, middle and ring portions of FDP were usually on the volar surface of the forearm directly above the relevant muscle (Fig. 1). For these sites, subjects rested their supinated forearm on the table. For the little (and occasionally the ring) portion of FDP, the forearm was held supinated and vertical while the electrodes were inserted from the medial side. To minimize discomfort, needles were inserted with the muscles relaxed and the digits held towards full extension. The needle was then removed, leaving the stiff wire electrodes 'hooked' into the muscle.

EMG in the test muscle during contraction of the lifting muscle was categorized as phasic or tonic. Phasic activity occurred only during the lift phase and tonic activity occurred during both the lift and hold phases. An example is shown in Fig. 2 in which no coactivation in the little digit portion of FDP occurred when weights equivalent to 2·5–5% MVC were lifted by the ring portion of FDP, phasic coactivation occurred for weights equivalent to 10% MVC, and tonic coactivation occurred for weights equivalent to 15% MVC. Categorization of the EMG was based on at least eleven lifts with data from the first three lifts excluded.

To obtain data for flexors of the five digits in seven subjects, approximately seventy-five electrodes were used. Three criteria had to be met before a recording site was acceptable. Firstly, the electrode recorded the activity from only one 'muscle' when the subject actively flexed at the distal interphalangeal joint against gravity. Secondly, the integrated EMG had to be linearly related to force when the subject contracted the test muscle isometrically to a force equivalent to 25% MVC. This was checked with the hand in the same position used to measure maximal force. When force was plotted against integrated EMG for each electrode site, linear correlation coefficients ranged from 0·91 to 0·99 (0·98 ± 0·02, mean ± S.D.). Thirdly, the electrode recorded single motor units at *low* forces (i.e. < 10 g at the mid-point of the distal phalanx). The two most common reasons for an electrode site to be rejected were: (i) the electrodes were not inserted sufficiently deeply and thus they recorded activity from superficial muscles, e.g. flexor carpi ulnaris and flexor digitorum superficialis, or (ii) the electrodes recorded activity from a different set of motor units when digits adjacent to the test digit flexed against gravity, i.e. the recording site was not 'selective' for one digital component of FDP (see Discussion). After most studies, the forearm was photographed with the electrode sites marked so that the crude topography of the deep digital flexors could be estimated. This was done to provide a map of the most appropriate sites and directions for electrode insertion and was especially useful when studies were repeated in individual subjects. When particular skin markings were noted they proved reliable guides for reinsertion of electrodes into the some digital components of FDP.

### Mechanical properties and morphology of FDP

Mechanical linkages between the digital tendons could confound the ability to move a distal phalanx independently of the other distal phalanges. Although rarely emphasized, there are tendinous slips in the forearm between the tendons of FDP and even between FDP and FPL (Rank, Wakefield & Hueston, 1968; Linburg & Comstock, 1979). To investigate this and the actual separation between the digital components of FDP and FPL, the forearms and hands of nine cadavers were examined. The presence of tendinous interconnections was

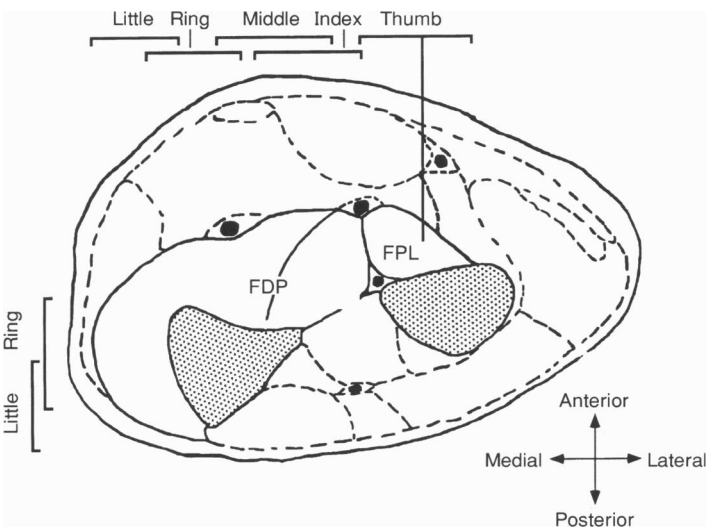


**Figure 1. Approximate sites for insertion of electrodes**
Cross-section at the mid-point of the forearm to indicate the location of FPL and FDP relative to the ulna and radius (shaded areas) and to the other muscles (dashed lines). Lines above and on anterior and medial sides indicate the electrode insertion sites for the five 'muscles' studied. This topography was based on photographs taken following each experimental session and uses data from each subject. The extent of vertical and horizontal brackets is intended to show the range of 'territories' for the components of FDP. Filled areas, major nerve trunks: in anteroposterior order, superficial branch of the radial, median, ulnar, anterior interosseous and posterior interosseous nerves.

noted and we measured the distance from the wrist to the most proximal point at which each major tendon was separate from its neighbours.

Motion of the distal phalanges was investigated *in vivo* under two additional conditions: (i) when a subject lifted a light weight with a digital component of FDP, and (ii) when the digits were fully paralysed and passively displaced. To measure displacement, a light stick (300 mm long) was attached to the nail of each digit, with the other end projecting back along the distal phalanx. Centred under the distal joints was a large protractor. When a subject ($n = 4$) voluntarily lifted a weight equivalent to 5% MVC with each digital component of FDP, flexion at the other distal phalanges acted on by FDP was measured. To investigate the properties of the muscles and tendons to passive movements, the arm was paralysed (and anaesthetized) distal to the elbow. A sphygmomanometer cuff was wrapped around the upper arm and inflated to 280 mmHg. Paralysis developed over 30–35 min. The paralysed forearm and hand were positioned as in the EMG study, and the tips of the digits were passively flexed and extended through the full range.

### Data analysis

In the EMG study, phasic (and tonic) coactivation thresholds were recorded as a percentage of MVC, i.e. the minimal weight lifted by one digit to produce phasic (and tonic) activity in the low-threshold motor units of the test muscle. Subjects did not lift weights greater than those that represented 50% MVC. Data were also coded according to the proximity between the test and the lifting digits. Thus, lifting with digits adjacent to the test digit (e.g. the little–ring finger combination) was equivalent to 1, two digits away (e.g. the little–middle finger combination) was equivalent to 2, and so forth. The Kruskal–Wallis one-way analysis of variance was used to determine whether coactivation was dependent on 'distance' between the test and the lifting digits and whether the coactivation threshold differed for particular digits. Data from each test muscle were also analysed separately to determine if the coactivation threshold was significantly related to (i) the lifting digit, and (ii) the type of coactivation (i.e. phasic or tonic). The Wilcoxon signed-rank test was used to determine whether there was reciprocity in patterns of coactivation between pairs of digits, e.g. was the coactivation threshold the same when the test muscle was middle portion of FDP and the index was lifting, and when the test and lifting roles were reversed? Lastly, analyses of variance of those cases in which a coactivation threshold was identified were used to compare the thresholds for different digits (i.e. threshold $\leqslant$ 50% MVC). Statistical significance was set at the 5% level.

## RESULTS

### Thresholds for coactivation

Subjects did not exhibit independent control of the muscles that flex the distal phalanges of the digits: coactivation occurred in the 'test' muscle if the 'lifting' digit lifted a sufficiently large weight (Figs 2 and 3). The same motor units recruited in the initial liminal contraction of the 'test' digit discharged phasically when an adjacent digit lifted a sufficient weight and discharged tonically when a larger weight was lifted. Coactivation could be abolished when a subject extended the test digit while lifting a weight with another digit. The coactivation thresholds were not due to an electrode recording activity from two digital portions (or two muscles) because one acceptance criterion for an electrode was that it only recorded low-threshold activity from one 'muscle' when the subject flexed without resistance at the distal interphalangeal joint (see Methods).

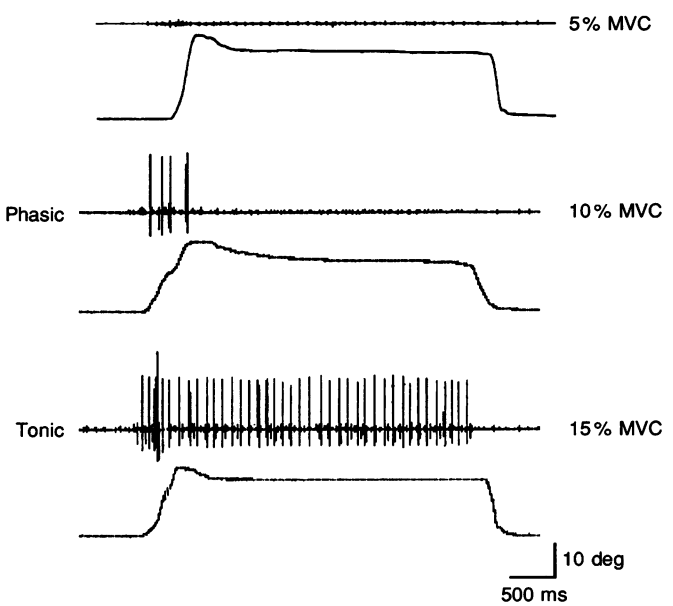


**Figure 2. Phasic and tonic coactivation**
Phasic activity occurred in the little finger portion of FDP when 10% MVC was lifted with the ring portion of FDP and tonic activity occurred when 15% MVC was lifted.

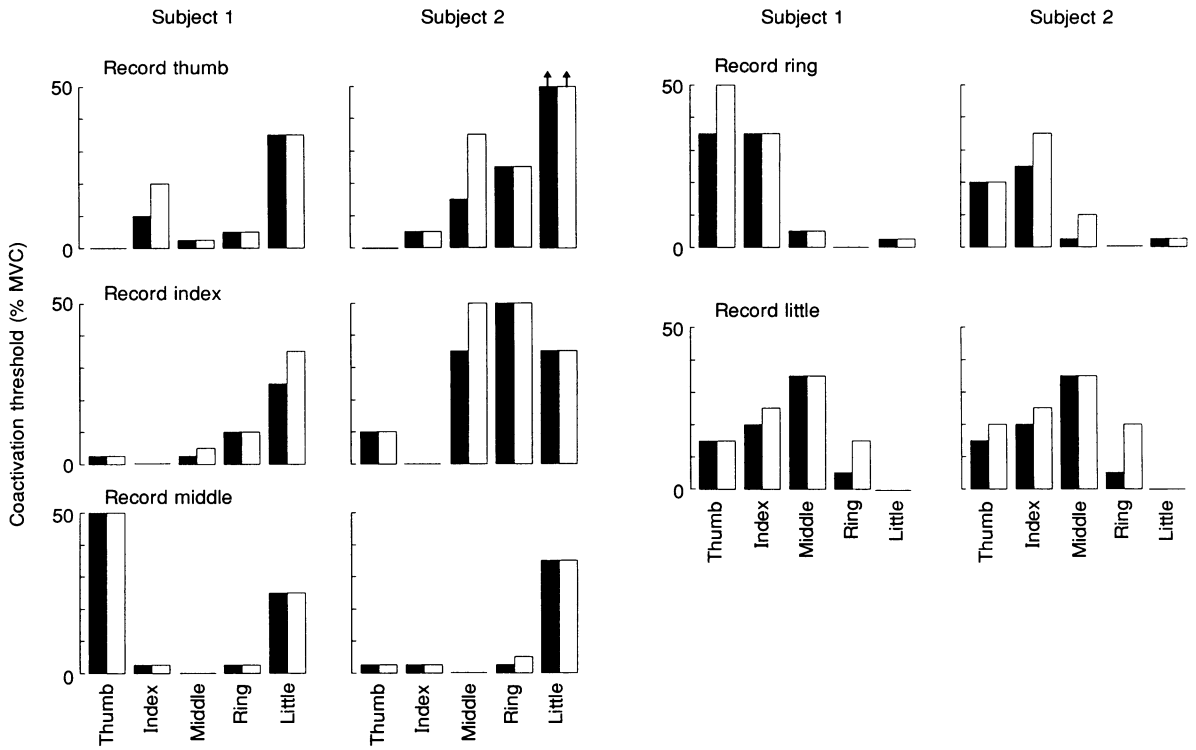


**Figure 3. Coactivation for two subjects**
Data from two subjects. Coactivation thrsholds for weights lifted by the 'lifting' digit to produce phasic (■) and tonic (□) EMG in the 'test' muscle. All weights lifted by flexion at the distal interphalangeal joint of the digits. The test muscle, i.e. that from which EMG was recorded, is indicated. Arrows indicate that coactivation was not present when a weight equivalent to 50% was lifted.

Integrated EMG was linearly related to force (up to 25% MVC) at each site for all digits. Thresholds for phasic coactivation were lower than for tonic coactivation in 32% of the 136 test–lifting combinations and the same in the remaining combinations.

Selective recordings from FPL and index portion of FDP usually required one electrode insertion. However, for the ring component of FDP, three to four electrodes per subject were usually required. In one of the seven subjects, even after five attempts, a site for selective recording of the ring component could not be located. In this subject, electrodes typically recorded activity in single motor units associated with flexion of two or three digits. An example is shown in Fig. 4. Presumably in the 'ring' portion of the muscle there was substantial overlap of the territories of motor units associated with adjacent digits (see Discussion).

The topography of the sites for selective recordings is estimated in Fig. 1, based on photographs taken of sites of electrode insertion in each subject. Recordings made at progressively more medial locations involved EMG associated with more medial digits. Selective recordings of the little digit component of FDP required electrodes in the posteromedial part of FDP and in the anteromedial part

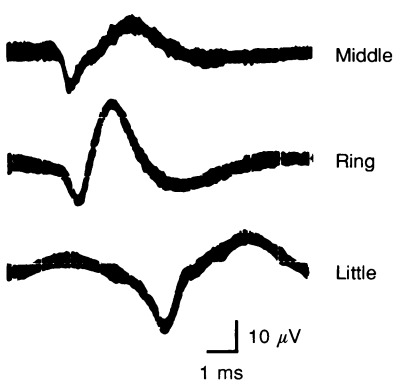


**Figure 4. Single motor units recorded from FDP**
Superimposed action potentials are shown for the lowest threshold motor unit recorded from a single electrode when each of the three digits flexed. A typical recording from a subject in whom it was not possible to find an exclusive ring finger site in FDP. Different motor unit potentials were recorded when the middle, ring and little digit flexed. These data suggest that the motoneurone territories for flexion of the three digits overlap.

for the ring component. The implied overlap in the figure of the sites for selective recordings may reflect intersubject variability as well as overlap among the territories of motor units associated with adjacent fingers.

The minimal weight lifted to produce coactivation in the test muscle, i.e. the coactivation threshold, was relatively low when the lifting digit was adjacent to the test digit: this pattern of coactivation thresholds is illustrated for two subjects (Fig. 3) and for the pooled data (Fig. 5). The data in Fig. 3 highlight the variability between subjects: when the middle digit lifted the weight, the coactivation threshold for the index portion of FDP was equivalent to 2·5% MVC for one subject but 35% MVC for the other. In twenty-six of the fifty-four adjacent test–lifting digit combinations, the phasic coactivation threshold was equivalent to 2·5% MVC (range 2·5–50%; see Fig. 5). However, when the lifting digit was three or four digits away from the test digit, no digital combination produced coactivation when weights equivalent to 2·5% MVC were lifted. Analyses of the pooled data showed that thresholds for both phasic and tonic coactivation were significantly related to the distance between the test and lifting digits (phasic: $\chi^2 = 66{\cdot}64$, degrees of freedom (d.f.) = 3, $P < 0{\cdot}001$; tonic: $\chi^2 = 61{\cdot}10$, d.f. = 3, $P < 0{\cdot}001$). However, analyses of variance of those cases in which the coactivation threshold was identified ($n = 117/136$) revealed that the threshold for coactivation was not significantly related to the test muscle, i.e. the coactivation thresholds recorded in the index portion of FDP did not differ significantly from those recorded in the ring portion of FDP. Thus, low-threshold motor units in muscles which are anatomically distinct (e.g. FPL and the index portion of FDP) were not activated more selectively (i.e. have higher coactivation thresholds) than portions of a muscle which are not anatomically distinct (e.g. middle, ring and little digit portions of FDP).

When analysed separately, each muscle showed the same significant trends: phasic and tonic coactivation in the test muscle was produced when relatively low weights were lifted by adjacent digits, and when relatively high weights were lifted by digits further away.

The relationship between the means of inverse pairs of data is plotted in Fig. 6 to investigate the 'symmetry' in the pattern of coactivation. The mean phasic coactivation threshold for a test–lifting digit combination is plotted against the mean threshold when the roles of the digits were reversed. The regression is significant ($r = 0{\cdot}87$; $P < 0{\cdot}001$). Thus, if the coactivation threshold is low for one test–lifting combination, it will be low when the roles of the digits are reversed. For all but one of the ten

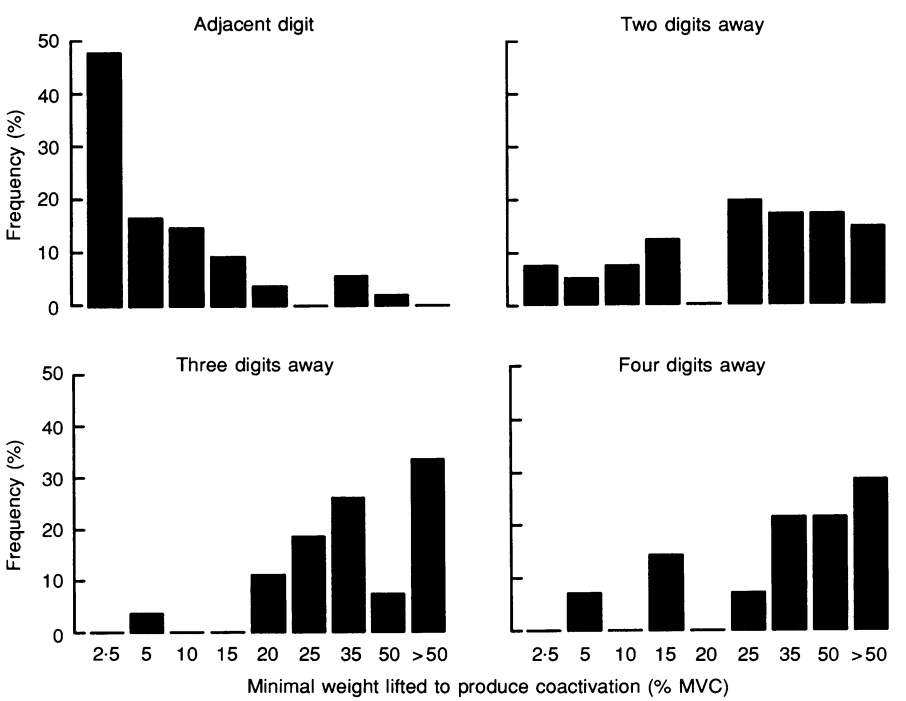


**Figure 5. Effect of distance between test and lifting digits on coactivation thresholds**
Frequency histogram of the minimal weight lifted to produce phasic coactivation of the test muscle, i.e. coactivation threshold. Data grouped according to the 'distance' between the test and lifting digits, i.e. adjacent digit (upper left panel; $n = 54$), two digits away (upper right panel; $n = 41$), three digits away (lower left panel; $n = 27$) and four digits away (lower right panel; $n = 14$). Coactivation of the test muscle usually occurred when light weights (equivalent to less than 15% MVC) were lifted by an adjacent digit, but was typically produced when heavy weights (greater than 20% MVC) were lifted by digits further away, e.g. three digits apart.

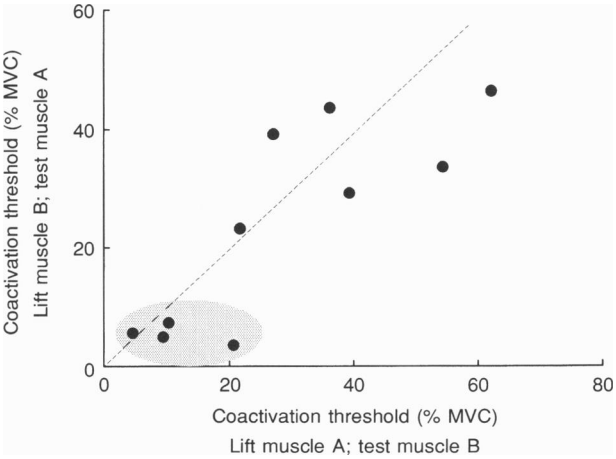


**Figure 6. Reciprocity of coactivation thresholds**
Mean phasic coactivation thresholds (expressed as a percentage of MVC) for one test–lifting digital combination plotted against the reverse of the combination. Dashed line indicates the line for symmetry. Four combinations in which the pairs of digits are adjacent are plotted within the shaded area. For pairs of data, the combination in which the test muscle is more radial (i.e. the thumb or closer to the thumb) is plotted on the $x$-axis, and the other combination is plotted on the $y$-axis.

combinations the coactivation thresholds did not differ significantly depending on which digit lifted the weight and which was the test digit (Wilcoxon signed-rank test). A significant difference in phasic coactivation threshold was noted only in the index–little digit combination ($P < 0{\cdot}05$).

## Factors affecting the coactivation threshold

Subjects routinely selected a comfortable constant angular velocity (in the range of 100–250 deg $s^{-1}$) and displacement (20–25 deg for thumb to ring digits, and 18–22 deg for the little digit) and used it for each lift. In eight experiments in which the weight was lifted slowly over five to ten trials (velocity 5–50 deg $s^{-1}$), coactivation decreased or was absent (Fig. 7*A*); in one subject, coactivation was not altered. Coactivation was also dependent on the angular range through which a subject lifted the weight. In seven (of eight) experiments, coactivation increased significantly as the amplitude of the displacement increased (Fig. 7*B*).

The presence of coactivation in the deep flexors was not critically dependent on the degree of restraint of hand position. The subject's fingers were usually stabilized by a bar across the dorsum of the middle phalanges, holding them against a vertical post. Removal of this restraint did not affect the coactivation thresholds for FDP when the thumb lifted weights (Fig. 8), nor for FPL when a digital portion of FDP lifted the weights. Likewise, in six subjects, the extent of coactivation in a digital portion of FDP was not affected when the proximal phalanx of the thumb was maintained against the pivoting point for lifting weights with the thumb. In one subject, additional stabilization of the thumb reduced the coactivation.

## Mechanical properties of FDP

With the forearm and hand anaesthetized by ischaemia, the hand was positioned to lift weights and each distal phalanx was passively displaced through the range used when lifting weights. The other digits did not move when

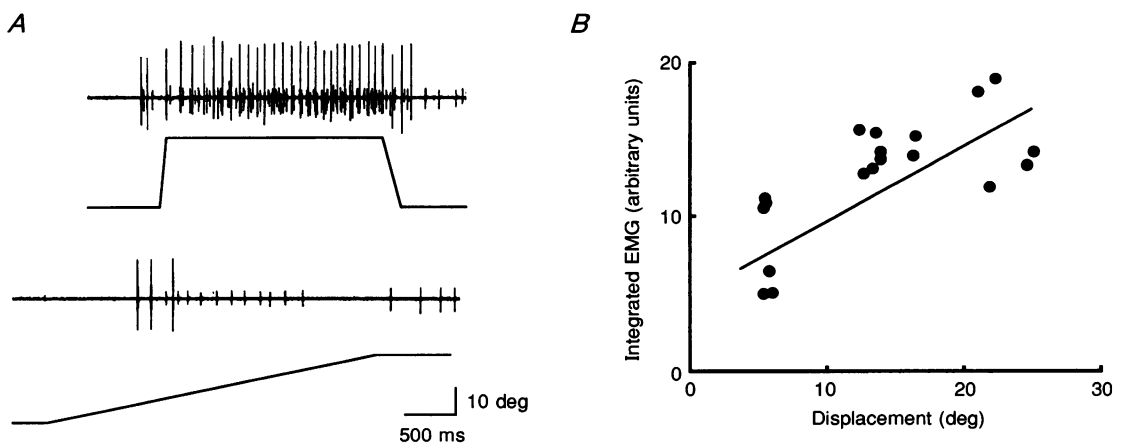


**Figure 7. Effect of velocity and displacement on coactivation**
*A*, a subject lifted a weight of 10% MVC with the thumb at two velocities, 125 and 32 deg $s^{-1}$, while EMG was recorded from the little digit portion of FDP. *B*, integrated EMG recorded from the ring portion of FDP when a subject lifted a weight equivalent of 2·5% MVC with the middle portion of FDP at an angular velocity of 50 deg $s^{-1}$. EMG increased as the displacement increased ($r = 0{\cdot}77$, $P < 0{\cdot}01$).

a digit acted on by FDP was passively flexed or extended. This occurred even when the hand was removed from the lifting apparatus and the fingers were extended at the metacarpophalangeal joints and the wrist extended. Thus, when the muscles are relaxed, movements of one digit are not transmitted inadvertently to its neighbours by friction between the skin surfaces of adjacent digits and there are no tight and incompressible links between adjacent tendons or muscle bellies.

This finding does not eliminate the possibility that significant mechanical interactions occur between FDP and FPL during active muscle movement. Two observations suggest that mechanical linkages cause movements at the distal interphalangeal joints of digits adjacent to the 'lifting' digit. Firstly, in the EMG study, when an adjacent digit lifted a weight, 'passive' movements of the test digit were observed occasionally in the absence of low-threshold EMG in the test muscle. Secondly, examination of cadavers ($n = 9$) revealed variable fine tendinous slips joining adjacent tendons of FDP in the distal forearm. In addition, adjacent muscle bellies associated with the four principal tendons of FDP were not completely separated. The length of separation of the tendons was measured as a distance proximal to the wrist. Separation of the tendons for the thumb (FPL) and the index portion of FDP ($131 \pm 42$ mm, mean $\pm$ S.D.), and between the index and middle portions ($111 \pm 21$ mm) extended much more proximally in the forearm than separation between the tendons to the middle and ring digits ($16 \pm 21$ mm) and between the ring and little digits ($34 \pm 38$ mm).

When subjects lifted weights equivalent to 5% MVC by flexion of each finger, with the hand in the position used for the EMG study, flexion of fingers adjacent to the lifting finger occurred (range 2–40 deg for all combinations). Such movement only involved adjacent fingers. Consistently large flexion movements of the ring finger were observed when the middle digit flexed (11, 12, 13 and 18 deg for the four subjects) compared with the low and variable amounts of movement observed in the other digital combinations. In the first part, when weights equivalent to 5% MVC were lifted, coactivation was produced in the adjacent test muscle in 73% of the combinations (excluding those combinations involving FPL; $n = 81$), while heavier weights had to be lifted to produce coactivation in more remote muscles (Fig. 5). Thus, when weights of 5% MVC are lifted by flexion at the distal joint of one digit, concurrent flexion of adjacent digits will usually reflect coactivation of adjacent 'muscles', but there may also be an effective 'in-series' link between tendons.

## DISCUSSION

The present study has shown that human subjects have a limited ability to contract selectively 'muscles' which flex the distal interphalangeal joints of the digits. There is an obligatory coactivation of other deep digital flexor muscles: this coactivation increases when the digit flexes at a greater velocity or through a larger angle. In half the studies in which the test and lifting digits were adjacent, low-threshold motor units in the test muscle were coactivated when a weight equivalent to only 2·5% MVC was lifted. When weights equivalent to 15% MVC were lifted by the adjacent digit, coactivation occurred in about 80% of the studies. Similar coactivation occurred in the

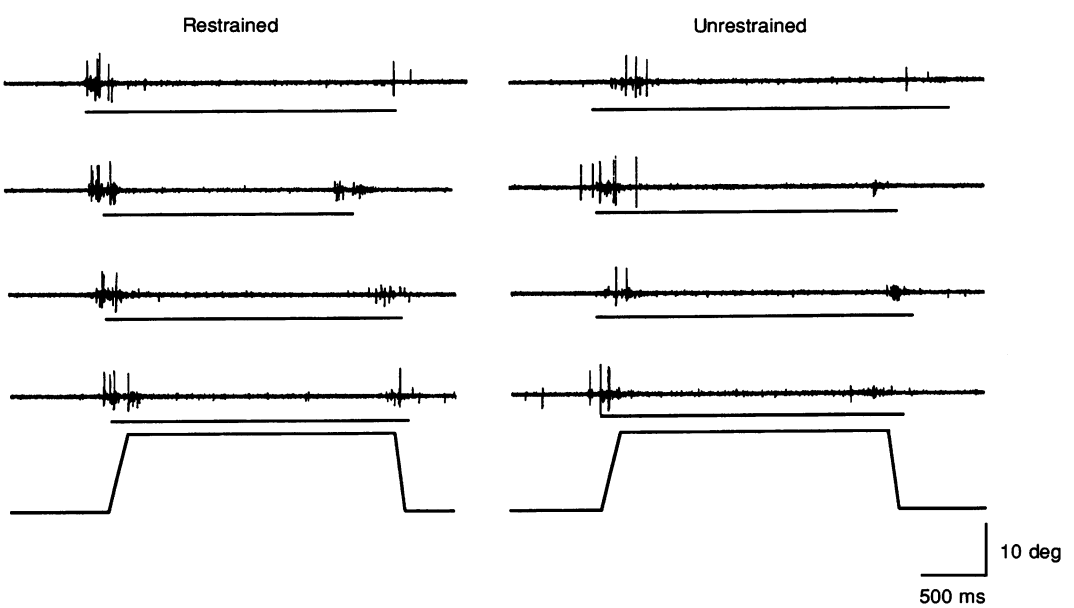


**Figure 8. Effect of restraint on coactivation**
Recording during consecutive lifts with and without restraint of the middle phalanges. Little digit portion of FDP recorded when 15% MVC was lifted with the ring portion of FDP.

test muscle (i.e. recruitment of the same motor units) when more remote digital flexors contracted, although heavier weights were required. This inadvertent coactivation was not dependent on the posture of the hand and subjects seemed unable to prevent it.

## Mechanisms underlying coactivation

Surprisingly, coactivation thresholds were not dependent on which muscle or digital portion of a muscle lifted the weight. For each test muscle, coactivation occurred when similar percentages of weight were lifted by adjacent digits. For example, when the test muscle was the index portion of FDP, phasic and tonic coactivation occurred when similar relative weights were lifted by the thumb and middle digits. When deliberate attempts were made to flex the distal joint of the thumb or of the middle finger, then the command 'spilt over' equally readily to low-threshold motoneurones innervating the index portion of FDP. If FPL received more selective neural drive during attempts to flex the thumb independently, a higher coactivation threshold should have been recorded when it lifted weights. This similarity between digits applies only to the *threshold* for coactivation. It may not apply to the *gain* of recruitment within the different pools of motor units in FDP or to other synergists. Coactivation thresholds increased as the distance between the test and lifting digits increased. This suggests that the commands to flex the distal joints of a single digit are somatotopically organized such that an increase in the command results in a 'spill-over' to progressively more remote digital flexors.

It is tempting to suggest that the lack of independence between the deep digital flexors reflects the known divergence of the corticomotoneuronal projections to functionally related motoneurone pools (Fetz & Cheney, 1980; Cheney & Fetz, 1985; Buys *et al.* 1986). Furthermore, cortical cells tend to be grouped according to function such that neighbouring cells facilitate the same target muscles (e.g. Cheney & Fetz, 1985; Cheney, Fetz & Palmer, 1985; Lemon *et al.* 1986). Presumably, the discharge of many cells with the same pattern of divergence could cause the motoneurones associated with the 'non-lifting' but functionally related muscles to fire. Based on a different experimental approach, the inability to control the excitability of individual forearm muscles selectively without producing a contraction has also been ascribed to the divergence in the corticospinal system (Gandevia & Rothwell, 1987). However, the present study does not explicitly reveal the underlying mechanism and it is likely that other descending paths mediating voluntary commands, perhaps via propriospinal neurones, show significant divergence and thus contribute to the coactivation reported here.

The lack of independent voluntary control over the deep digital flexors occurred despite intact cutaneous and muscle reflexes. Cutaneous reflexes from the human hand exert both short- and long-latency reflex effects on muscles which move individual digits (e.g. Caccia, McComas, Upton & Blogg, 1973; Jenner & Stephens, 1982; Aniss, Gandevia & Milne, 1988), and somatotopically organized cutaneous reflexes exist for the cat paw (Hongo, Kudo, Oguni & Yoshida, 1990). The complex architecture of cutaneous reflexes can presumably favour either more selective movements of individual digits or co-operative movements such as movement of the thumb and index finger (e.g. Gandevia & McCloskey, 1977). Edin, Westling & Johansson (1992) have recently shown that humans can control two finger tip forces independently when they contact surfaces with different frictional properties. The cutaneous reflex organization of FDP and FPL has not been investigated in detail in human subjects, although an important facilitation has been identified (Gandevia & McCloskey, 1977; Marsden, Merton & Morton, 1977; Loo & McCloskey, 1985).

We also considered the possibility that muscle spindle and Golgi tendon organ afferents are important for the relatively independent activation of the deep digital flexors. However, both classes of afferents have divergent connections onto homonymous and heteronymous motoneurone pools (e.g. Eccles, Eccles & Lundberg, 1957; Brink, Jankowska, McCrea & Skoog, 1983; Fritz, Illert, de la Motte, Reeh & Sagau, 1989). As yet, no data on sensory and reflex partitioning of muscle afferent input in humans are available for FDP to assess the possibility critically. In the cat, reflexes from spindle afferents in FPL and the digital components of FDP are bidirectionally interconnected and any reflex partitioning within FDP is not strong (Fritz *et al.* 1989). In humans, the extent of reflex connections from muscle spindle afferents in FDP is not clearly established (cf. Matthews & Miles, 1988). It is unlikely that fusimotor outflow is sufficiently selective to focus the relevant motor commands via spindle-mediated facilitation, given the complex mechanical interactions (see below), in-series connections of spindles, and the likelihood of spindle unloading during shortening contractions (Al-Falahe, Nagaoka & Vallbo, 1990; cf. Burke, Hagbarth & Löfstedt, 1978). Even if the combination of topographically organized spindle and tendon organ feedback does serve to 'focus' the descending commands to one portion of FDP, it breaks down when forces exceed 5% MVC and coactivation becomes widespread.

Given the degree of coactivation between digital portions of FDP and FPL, how then is independent digit movement achieved? The present study has only analysed coactivation among the muscles which flex the distal joints in a situation which usually eliminated the contribution from other muscles including the intrinsic muscles, flexor digitorum superficialis and extensor digitorum communis. Presumably their actions, and particularly those of the intrinsic muscles, contribute to focal movement of the digits, a view for which there is experimental support. Simultaneous recordings from first dorsal interosseous, index portion of FDP, adductor pollicis and FPL when

weights equivalent to 10% MVC were lifted showed that coactivation did not occur between adjacent intrinsic muscles (first dorsal interosseous and adductor pollicis) while it was present for the two extrinsic hand muscles (see Fig. 2 in Kilbreath & Gandevia, 1993*b*). The ability to recruit and control the discharge of single motor units innervating intrinsic hand muscles, even when the muscles were paralysed and their muscle afferent feedback removed, supports this idea (Gandevia, Macefield, Burke & McKenzie, 1990). Furthermore, studies here were only able to investigate the threshold for coactivation and did not measure recruitment of forces beyond those which initiated coactivation.

## Mechanical linkages between 'muscles'

There are mechanical interconnections between the muscles which flex the distal joints of the digits. In humans, FPL and the digital portions of FDP 'show definite cleavage into three divisions' (Wood Jones, 1949; see Fig. 1): (i) FPL arises from the radius, (ii) index portion of FDP arises from the interosseous membrane, and (iii) the middle, ring and little digits component arises from the ulna. Thus, contraction of one portion of FDP, e.g. middle, ring or little digit portion, could mechanically shorten the adjacent compartments. Furthermore, there are tendinous slips in some subjects between adjacent tendons of FDP (e.g. Rank *et al.* 1968; confirmed here), even between FPL and the index portion of FDP (e.g. Linburg & Comstock, 1979).

When muscles in the forearm and hand were paralysed, passive movement of the tips of the digits resulted in no movement of the other digits. A comparable assessment in the monkey was considered by Schieber (1991) to rule out the possibility of significant mechanical interactions causing distributed flexion of more than the lifting digit. Given the known intertendinous connections and properties of contracting muscle, such an approach on its own is insufficient. Direct evidence that mechanical linkages could affect movement of the digits includes the following. Firstly, movement of a test digit was occasionally observed in the absence of low-threshold EMG when the adjacent digit lifted weights. Against this, it is possible that the electrodes did not record the lowest threshold motor units. Secondly, separation of the major tendons of FDP occurs close to the wrist for the middle–ring and ring–little components of FDP. Furthermore, in humans, connections between the deep flexor tendons can also occur in the palm (Rank *et al.* 1968) and this would further disperse contractile forces to more than the 'lifting' digit. In the macaque monkey the divisions of FDP into separate tendons for all of the digits (including the thumb) occurs at or just beyond the wrist (Serlin & Schieber, 1993).

We have loosely referred to components of FDP which flex individual digits as 'muscles', although it is unlikely that there are absolute criteria which define a muscle, particularly when multitendoned structures are considered (Windhorst, Hamm & Stuart, 1989). FPL and FDP can be considered distinct muscles, with different characteristics: FDP is multitendoned, with the index portion enclosed in fascia, and anatomically distinct from the middle, ring and little finger components. However, the similarity in coactivation thresholds for the five digits suggests that, at least for the low-threshold motor units, these anatomical considerations are of little neurological consequence.

It might be argued that FDP is four separate muscles, each acting on one digit. From the data presented here, this appears unreasonable. To test the selectivity of electrodes inserted into the muscle belly of one digital portion of FDP, a subject initially attempted to flex each distal joint against gravity. The electrode was considered selective if EMG was recorded only when the test digit flexed, but often EMG was recorded when adjacent digits flexed; that is, activity was recorded from other motor units and/or the 'test' units. When this occurred, the electrodes were removed and this accounted for the high number of electrodes used (see Methods). Different motor units associated with adjacent components of FDP would be recorded if the unit territories overlapped or the electrodes were insufficiently selective. Overlapping motor unit territories probably occurred towards the medial side of FDP. Whereas one or two electrode insertions were usually required to record selectively from FPL and the index portion of FDP, three or more were often required for the ring and middle portions. In one subject, the ring component could not be recorded selectively after insertion of five new electrodes (Fig. 4) and there were different motor unit potentials recorded on attempted flexion of the ring, middle and little fingers. This finding suggests that the degree of mixing of motor units might vary between subjects. Another factor to consider is the possibility that a single motor unit could act mechanically on adjacent digits. In the cat forelimb, motor units of extensor digitorum communis distribute their force preferentially but not exclusively to one tendon (Fritz & Yamaguchi, 1985). This may be particularly relevant for the more medial parts of FDP.

In conclusion, the deep long flexors of the digits cannot be selectively contracted, even when cutaneomuscular reflexes, which may favour selective movements, are present. This limited independence is likely to reflect effective divergence of the motor commands to these muscles. Anatomical links which are effectively 'in series' also serve to distribute flexor forces to adjacent digits.

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